Reproductive Biology of the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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Poorly known aspects of external dimorphism, maturation, early development and the annual reproductive cycle of *Euastacus spinifer* have been investigated in populations south of Sydney (Georges River, Hacking River, Loddon River). Setal development surrounding gonopores is a reliable field indicator of maturity in females and the degree of inflation of genital papillae is a useful maturity indicator in males.

Females commence maturing at 65 mm carapace length (CL), but many don't mature until 70–75 mm CL; a majority spawn once each year after reaching maturity. Two groups of reproductively functional males were identified in Loddon River populations; normal males became functionally mature at 45–55 mm (CL), but small 'precocious' individuals were mature at 12–20 mm CL.

The robust spermatophore structure is considered to be related to the protracted period (4–6 weeks) between mating and release of the ellipsoid, yolky eggs (means 3.5, 2.7 mm); fecundity increased with size (268 at 73.1 mm CL to 1299 at 109.4 mm CL). Early embryonic development and the three juvenile stages between hatching and release are similar to those of other parastacids; development of offspring on individual *E. spinifer* females is synchronised.

In the Loddon River mating occurs in late May or early June when water temperatures fall rapidly below 15°C. Most breeding females are carrying spermatophores in early June and eggs by early July; incubation extends for 110–140 days over winter. Juveniles remain with the parent for a further 28–70 days before release in early December (water temperatures 20–24°C). Timing of events in this annual cycle is known to vary in different river systems; however, *E. spinifer* is clearly a winter brooder. The selection mechanisms, that may have produced the precocious males remain unknown.

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KEYWORDS: Reproduction, *Euastacus spinifer*, dimorphism, maturation, development, seasonality.

INTRODUCTION

Australia's freshwater crayfish fauna is diverse but poorly known (Merrick 1993) and detailed studies of the group have been restricted (largely) to a few species that are significant in recreational fisheries or have commercial culture potential (Merrick and Lambert 1991). Aside from original descriptions and isolated natural history comments there is virtually nothing published on most mainland species — many of which have restricted ranges in the eastern highlands and coastal drainages (Merrick 1993, 1995).

As part of an extended program on growth and population structure in *Euastacus spinifer* several aspects of reproduction were investigated; the only other *Euastacus* species whose reproductive biology has been studied comprehensively are *E. armatus* (Geddes 1990; Geddes et al. 1993; Morgan 1986) and *E. bispinosus* (Honan and Mitchell 1995a, b, c). Table 1 provides selected reference data for 18 *Euastacus* species.

TABLE 1

Selected reproductive data for *Euastacus* species, aside from *E. spinifer* (from Honan and Mitchell 1995a; Jones and Morgan 1994; Merrick 1993, 1995; Merrick and Lambert 1991; Morgan 1986, 1988, 1997; Turvey 1980).

Species	Size at maturity (CL in mm)*	Fecundity (Egg size in mm)†	Mating & Spawning Season	DEVELOPMENT		
				Incubation (Period)	Larval Period	Release
E. armatus	40 (♀)	300–800	May–June	June–October (4–5 months)	October–November (3–4 weeks)	November–December
E. australasiensis	30–40 (♀)	44–155 (3.0, 2.0)	Autumn	May–October (4–5 months)	September–November	September–January
E. balanensis	~30 (♀)			Winter		
E. bispinosus	55–85 (♀)	63–812 (<4.1 long)	April–May	June–October (6–7 months)	October–November (4 weeks)	November–December
E. crassus	50–60 (♀) 30–40 (♂)			November–March	February–April	
E. gumar	>30 (♀)			September		
E. hystricosus	~60 (♀) ~40 (♂)		Autumn	May–September		
E. keirensis (now synonymised with *E. hirsutus*)	30–40 (♀)	55–184	Autumn	May–November	Summer	
E. kershawi	65–70 (♀) ~50 (♂)	1000–1200				
E. reductus	~30 (♀)			September–October	January	
E. robertsi	60 (♀)			September		
E. setosus	30 (♀)			October		
E. sulcatus	40 (♀) 30 (♂)		Autumn	Winter		
E. suttoni	40 (♀) 20 (♂)		Spring		Summer	Late Summer
E. valentulus	>40 (♀)			May–October	October–November	
E. woiwuru	40 (♀)			September		
E. yanga	30–50 (♀)	43–164		October–November		
E. yarraensis	~40 (♀)			September–November		

*These carapace lengths are rounded and indicate minimum size at sexual maturity; these values are equivalent to the commonly quoted OCL. Some species mature over a wide size range and maturity sizes vary in different populations.

†Where eggs are described they are ovoid or ellipsoid.

Dimorphism, Maturation, Early Development and the Annual Cycle

The sexual dimorphism seen in many decapods (Barnes 1987) is not marked in parastacids. The external reproductive morphology of parastacids, has been described previously in taxonomic works (Riek 1969, 1972); gonopores of females are located on the coxae of the third pereopods, while male gonopores are produced into papillae on the coxae of the fifth pereopods. In several larger *Euastacus* species females are reported to have broader abdomens and males to have larger chelae (Jones and Morgan 1994); these differences conform to the patterns of differential allometric growth, between the sexes, described in other crayfishes (Lowery 1988).

In order to relate variation in *E. spinifer* growth rates to sex and size, it was essential to reliably determine (in the field) the state of maturity of captured individuals without harming them. Mature females of other parastacids have been identified by the presence of attached eggs during the breeding season (Shipway 1951a,b), or by the presence of egg-bearing setae on the pleopods (Morrissy 1970). Mature males have not been reported to exhibit external maturity features; however, Shipway (1951a) noted that the genital papillae of male *Cherax tenuimanus* become more erect during the mating season. In small samples of large *Euastacus* females Ryder (1972) noted that gonopores were surrounded by setae and, at the commencement of this study, considerable variation was observed in the degree of inflation of genital papillae of *E. spinifer* males.

Unpublished observations on spermatophore structure in *Cherax destructor* are available (Johnson 1979), but aside from several general comments by Honan and Mitchell (1995a), there are no published studies of *Euastacus* spermatophores. The few observations of *Euastacus* eggs describe them as being maroon, reddish-brown or orange in colour and ovoid or ellipsoid in shape; egg colour is also reported to change during development (Merrick 1993; Morgan 1988; Turvey 1980).

Aspects of the reproductive cycle have been described for a few species in several other parastacid genera (Hamr 1990, 1995; Lake and Newcombe 1975; Morrissy 1970, 1975; Suter 1977); however, except for *E. bispinosus* (Honan and Mitchell 1995a), there has been no systematic investigation of *Euastacus* relating major physicochemical environmental influences to gonadal maturation, breeding or early development over several annual cycles. Parastacid breeding cycles have been recently discussed by Hamr and Richardson (1994) and Honan and Mitchell (1995a).

This paper is the first in a series on the biology of the Sydney crayfish *Euastacus spinifer*. Objectives of the studies reported here are: to establish whether the development of setae surrounding the gonopores can be used as a reliable field indicator of female maturity; to ascertain whether the degree of inflation of genital papillae in males can be used as a field indicator of maturity; to relate phases of reproduction or development with major environmental parameters and demonstrate factors which may influence the reproductive cycle; and to discuss the overall life cycle strategy of *Euastacus spinifer*.

MATERIALS AND METHODS

Observations were made on several populations; however, most data were derived from the Loddon River population. Crays were captured using baited drop-nets and individual size determined by measuring carapace length (CL) to the nearest 0.1 mm, from the posterior margin of the orbit to the middle of the dorsal posterior carapace margin; all CL, gonopore and egg dimensions were measured with dial calipers. Captured specimens were marked for recognition by removing distal portions of the abdominal pleura and tail fan, according to the system illustrated in Turvey and Merrick (1997a).

Study Area

The Loddon River is the most eastern tributary of the Nepean River system and forms part of the catchment of the Cataract Dam under the jurisdiction of Sydney Water; public access is restricted and most of the catchment is in a natural condition. The Loddon originates on the plateau behind the Illawarra escarpment in a shallow basin, with an area of approximately 13 km^2 at elevations of 360–380 m (lat. 34°17′S: long. 150°54′E).

The river commences as a series of small, semi-permanent channels draining the sedge swamp which covers much of the basin and overlies Hawkesbury sandstone. This swamp is thought to have been in its present state for a long period (Davis 1936), maintained by a combination of high rainfall and high water table resulting from slow evaporation rates, the local soil structure and vegetation, as well as the presence of furrows (at intervals of 0.9–1.8 m) at right angles to the normal drainage slope. The soil layer is deep, (up to 5.0 m) with an acid pH and high humus content.

The main watercourse commences abruptly, in the south-western sector of the swamp, as a series of large pools connected by shallow riffles and narrow channels. The area sampled comprised the first eight of these pools, extending approximately 500 m downstream but with little gradient. The pools (30–100 m in length, up to 30 m in width), consist of channels excavated through the sedge swamp to the bedrock at depths of 4 m or more. Banks are characteristically almost vertical, extending from less than 1 m above water level to depths of 3 m, and flow rates are negligible except during times of flood.

The stream bed consists of flat shelves of sandstone, irregular outcrops and boulders, interspersed with areas of sand and gravel. The bottom was typically clean in appearance; plant debris was sparsely and patchily distributed, with substantial accumulations in restricted areas. The only conspicuous vegetation consisted of dense, but narrow, stands of the aquatic angiosperm *Triglochin procera* (ribbon weed) along the edges of some pools with less steep banks.

Aside from a typical assemblage of insects, the only aquatic macroinvertebrates observed were the shrimp *Paratya australiensis* and another small crayfish, *Euastacus keirensis* (now synonymised with *E. hirsutus* by Morgan (1997)). The two major fish species present were mountain galaxias and Macquarie perch.

Maturation

Females

Females (CL range 20–100 mm) were collected from the study area in 1976, 1977, and 1978 during May and June, just prior to spawning. These specimens were returned to the laboratory, anaesthetised by chilling, and weighed (to nearest 0.1 g); ovaries were then removed under a dissecting microscope. Adherent blood vessels were cut away and oviducts severed at the points at which they turned ventrally around the lateral margins of the hepatopancreas. The gonads were drained briefly on tissue paper and weighed (nearest 1 mg); the contribution of reproductive tissues to body weight was expressed for each crayfish as a 'gonosomatic index' of the form:

$$[\text{gonad weight}/(\text{body weight} - \text{gonad weight})] \times 100.$$

Changes in gonosomatic index associated with body weight were determined.

The second left pleopod and coxa of the third left pereopod were also removed from each dissected female and fixed in formol-alcohol (Humason 1972). Major types of setae surrounding the gonopores and on the pleopods were described, classified according to Thomas (1970), and distributions recorded. Three patterns of setal distribution (Stages 0, 1 and 2) were proposed and each cray allocated to a stage from observation of the gonopore.

All females examined were allocated to CL classes (5 mm increments) and percentages of individuals in each size class at each setal Stage calculated. Confidence limits (95%) for values on repeated sampling were estimated for each percentage using a normal approximation for samples exceeding 30 individuals, in each size class (Snedecor and Cochran 1967), or from tables based on the binomial distribution (Crow 1956) for smaller samples.

Another 20 females (in Stages 1 and 2) were examined in the laboratory during November or early December in 1976 and 1978. Numbers in each stage with developing, yolky oocytes and immature oocytes were determined and Stage 1 was further sub-divided. These laboratory results were supplemented with field data; females examined in the field were considered mature when they were known to have spawned, but the mark-recapture records also provided setal allocations of immature females. Setal stages were compared between captures for each individual that was captured more than once and inconsistencies in allocations, that could not be explained by transitions at moulting from Stage 0 to Stage 1 or Stage 1 to Stage 2, were noted.

The maximum diameter (to nearest 0.1 mm) of the left gonopore was measured for each of a series of females.

Males

Males in the range 20–90 mm CL were collected from the study area in 1976, 1977 and 1978 in May, during the mating period; these individuals were anaesthetised by chilling and weighed (nearest 0.1 g). Both testes and vasa deferentia were removed, under a dissecting microscope, after cutting away adhering blood vessels and severing the vasa deferentia close to the gonopores. Gonads were drained briefly on tissue paper, weighed (nearest 1 mg), fixed for one hour in alcoholic Bouin's solution (Humason 1972), and stored in 70% alcohol. Gonosomatic indices were calculated as for females. Paraffin sections 10 μm thick were taken at several places along the posterior lobes of the testis and stained in Delafield's hematoxylin and eosin by the regressive method (Humason 1972). Mature males were identified by the presence of sperm in open spermatic cysts and ducts in the testis.

Males were divided into three groups on the basis of the degree of genital papilla inflation and the relationships between papilla inflation, maturity and gonosomatic index were investigated. All males captured were size classed (using 5 mm CL increments) and further classified by papilla development status; percentage abundances of each inflation state, related to size, were examined.

Records of marked individuals, that were captured more than once, were examined for variability in the degree of inflation of genital papillae through time.

Spermatophores, Fecundity and Early Development

The appearance of spermatophore material was described before and after its attachment to females, and the structure of attached spermatophores was examined from sections (0.5 mm thick) of fresh material.

Eggs, egg attachment, juvenile stages and juvenile attachment were briefly described. Maximum and minimum diameters (to nearest 0.1 mm) of 10 eggs from each of five females were measured for estimates of egg size. The relationship between egg number and the size of females was estimated as the linear regression of egg number on carapace length for 10 individuals.

Annual Reproductive Cycle

Events in the annual reproductive cycle of *E. spinifer* were described from the condition of mature females captured each month as part of the mark-recapture study of

growth. Mature females were identified upon capture and rated according to whether they were carrying spermatophores, eggs, or first, second or third stage juveniles. Individuals were assigned a brooding state and specimens with each state tabulated for each month; combined raw data for the three years were compared.

Average water temperatures were recorded for each monthly sampling at two of the pools for the period May 1977 to December 1978. Periods during which mating, spawning and release of juveniles occurred were compared with the annual water temperature regime.

RESULTS

Maturation

Females

Ovary Structure

The ovary of *E. spinifer* is located ventral to the heart, dorsal to the hepatopancreas, mid- and hindgut, and posterior to the gastric mill, extending slightly into the first abdominal segment. Each ovary consists of two elongate, tubular sacs joined by a single, broad commissure towards the anterior end, adjacent to the points of exit of the oviducts. As oocytes mature prior to spawning, the ovary increases in size to occupy much of the posterior cephalothoracic lumen. The yolk of mature oocytes is a maroon to dark maroon colour; white oocytes observed have been classed as non-yolky.

Setation

Setae surrounding the female gonopores are mostly of the pappose type (Fig. 1); each seta consists of a thick, tapering shaft with numerous, distally-directed setules distributed irregularly around the shaft circumference. By contrast, the setae on pleopod margins are of two types, plumose setae and oosetae (Fig. 1). Each plumose seta comprises a shaft of moderate thickness bearing numerous, long, distally-directed setules arranged in opposing pairs, in the same plane as flat surfaces of the pleopod. Each ooseta consists of a long, filament-like shaft bearing a number of minute setules over its distal quarter; these setules are barely visible even at 400x magnification.

Females were allocated to one of three stages on the basis of the patterns of setae around the gonopores (Fig. 2). Crayfishes in Stage 0 lack obvious setae around the gonopores. Basipodites of the pleopods are free of obvious setae, while all margins of both endopodites and exopodites carry a continuous fringe of evenly-spaced plumose setae. Stage 1 is recognised by partial encirclement of each gonopore by a narrow band of pappose setae. Setae are typically distributed sparsely within this band, although in some individuals they are arranged in dense but narrow clumps for short intervals, particularly around the posterior gonopore margins; both plumose setae and oosetae are present on the pleopods. Oosetae and a few plumose setae are present on the medial margin of the basipodite, the lateral margin of the near-proximal exopodite, as well as medial and lateral margins of the near-proximal endopodite; otherwise both endopodite and exopodite carry the complement of plumose setae typical of Stage 0. The presence of oosetae usually corresponds to a reduction in the number of adjacent plumose setae in Stage 1 females.

Stage 2 individuals have complete encirclement of each gonopore by a band of pappose setae (Fig. 2). These setae are frequently longer posteriorly, and the band of setae is narrower anteriorly in some smaller individuals. Otherwise, setae are densely packed to form a continuous band up to several millimetres wide around each gonopore; in large specimens, a dense belt of setae frequently extends anteriorly over the surface of the coxa.

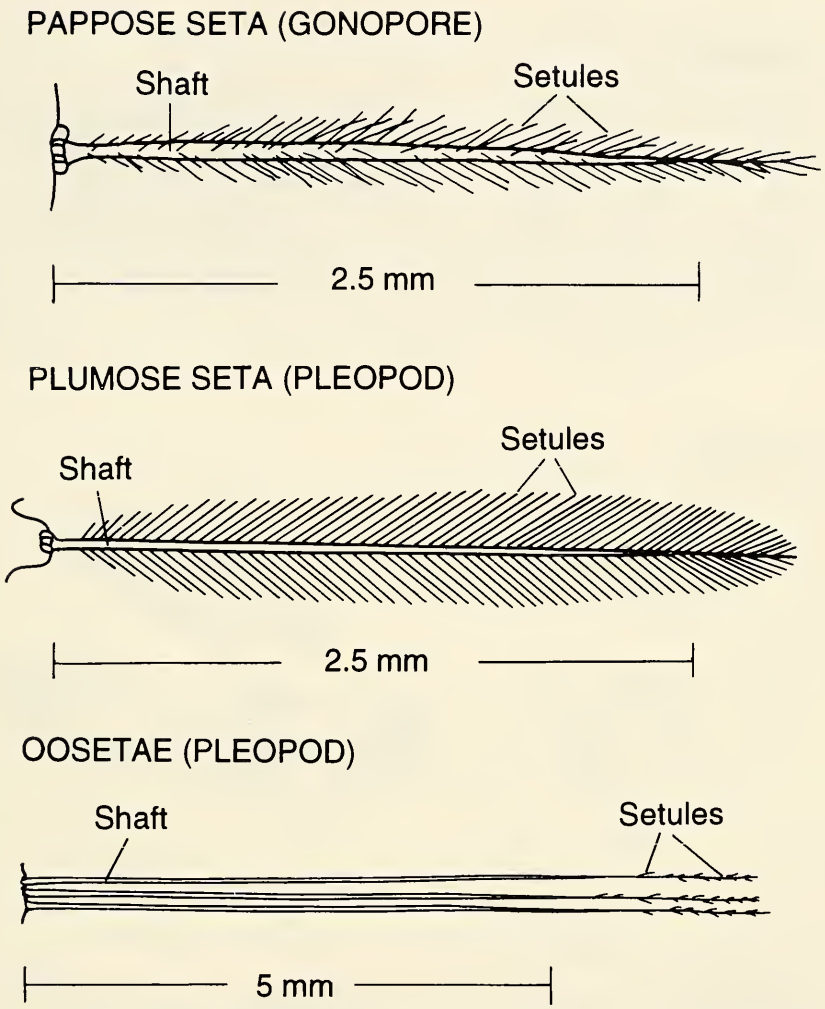

Figure 1. Major types of setae surrounding gonopores and on the pleopods of mature *E. spinifer* females.

Dense beds of long oosetae are conspicuous on pleopods of Stage 2 females. Oosetae are best developed on the medial margin of the basipodite, lateral and medial margins of the proximal endopodite and lateral margin of the proximal half of the exopodite. Plumose setae are either very sparse or absent in these areas and oosetae are typically twice the length of plumose setae elsewhere on the pleopods. Shorter oosetae are usually present on the central third of the lateral margin and proximal two-thirds of the medial margin of the exopodite, as well as all margins of the distal endopodite except the tip.

The presence of oosetae in these areas corresponds to a reduced density of plumose setae similar to that described for Stage 1 females, while the very tip of the endopodite and distal third of the exopodite carry plumose setae typical of Stage 0. The described oosetal patterns are applicable to most individuals in Stages 1 and 2; however, oosetal development in some Stage 1 specimens was indistinguishable from Stage 2.

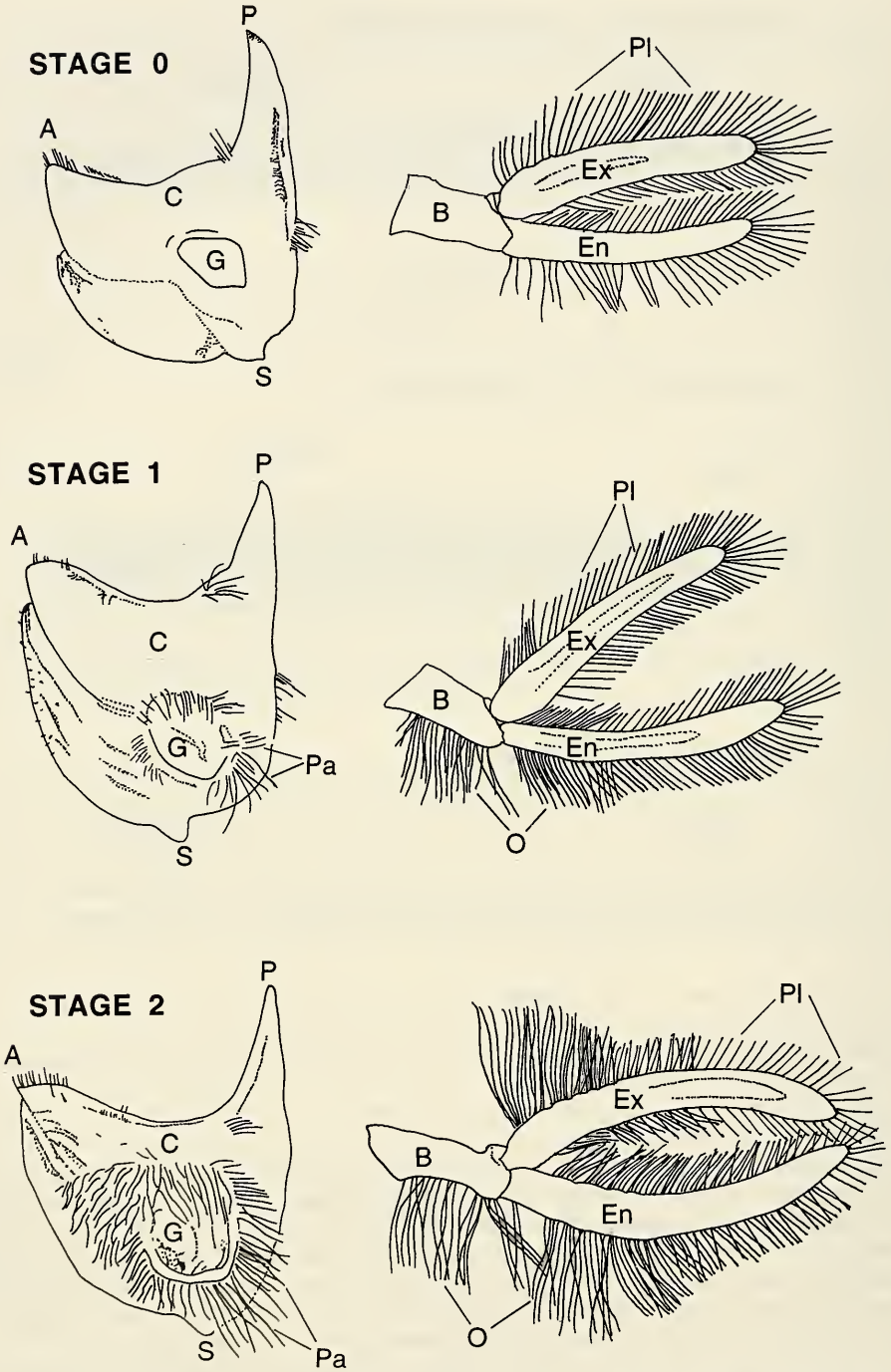

Figure 2. Patterns of setae around gonopores and setal distributions on the pleopods of female *E. spinifer*. Left field: ventral view of the coxa of the left third pereopod; right field: anterior view of the left second pleopod. Key to abbreviations: A = anterior articulation of coxa with basis (or basipodite); B = basipodite; C = coxa; En = endopodite; Ex = exopodite; G = gonopore; O = oosetae; P = posterior articulation of coxa with basis; Pa = pappose setae; Pl = plumose setae; S = articulation of coxa with sternum.

Gonosomatic Index

This index, ovarian maturity, and setal stage were clearly related for females examined just prior to spawning. Data were plotted with indices scaled in $\log_{10}$ to provide approximately linear relationships with body weight (Fig. 3). All Stage 0 and Stage 1 individuals had immature ovaries, while in nine of the ten Stage 2 females the ovaries were mature. Oocytes in the other Stage 2 female were normal in appearance and light yellow-orange in colour, indicating early stages of yolk deposition, so the ovary was classified as developing. The gonosomatic indices of Stage 0 and Stage 1 females formed a continuous, approximately exponential progression with body weight from approximately 0.02 at ~10 g, to approximately 0.3 at a body weight of 300 g. In contrast, gonosomatic indices of Stage 2 females were much higher and, on average, constant with body weight (2.5–3.0); the index of the Stage 2 female with a developing ovary was similar to indices of Stage 1 individuals of similar size.

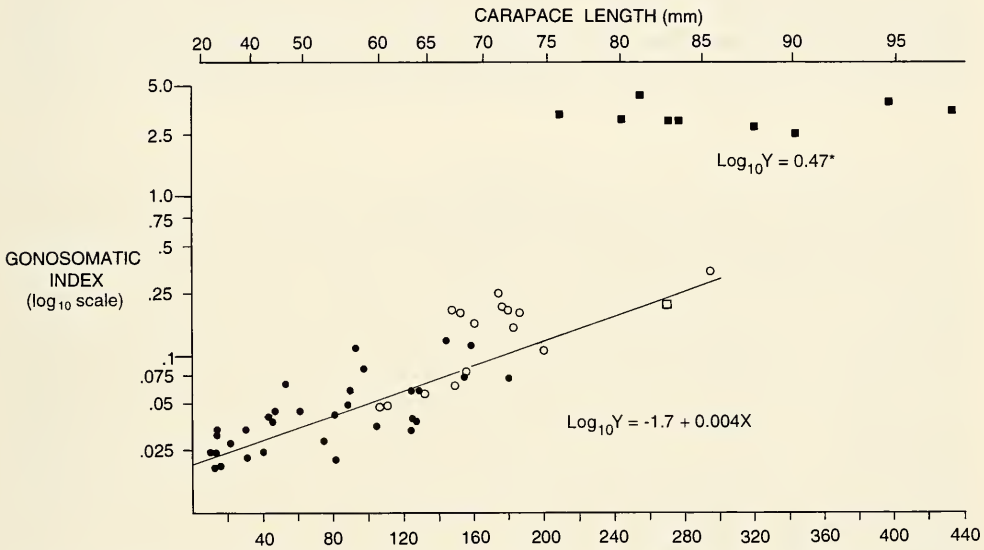

Figure 3. Relationship between gonosomatic index, ovarian maturity, setal stage and body weight in female *E. spinifer*. Key to symbols: ● = Setal Stage 0, ovary immature; ○ = Setal Stage 1, ovary immature; ❑ = Setal Stage 2, developing ovary; ■ = Setal Stage 2, mature ovary. * slope of regression for mature individuals not significantly different from zero ($p >> 0.5$), but slope of regression for immature individuals significantly different from zero ($p << 0.001$).

In addition, 71 mature females were examined in the field. In 69 instances individuals were allocated to Stage 2 and the other two were allocated to Stage 1; but both of these females had been allocated to Stage 2 on several other occasions. There were also occasional inconsistencies in the field allocation of females to Stages 0 and 1. Of 112 records of Stage 0 individuals, that were captured more than once, there was a single inconsistent allocation of an otherwise Stage 0 female to Stage 1; out of 31 captures of Stage 1 females there was also a single allocation of a Stage 1 specimen to Stage 2.

Among females captured and dissected during November to December, all eight Stage 2 individuals and eight of the 12 Stage 1 specimens had ovaries containing yolky, developing oocytes; remaining Stage 1 animals had ovaries containing non-yolky, immature oocytes. It was not possible to distinguish between the Stage 1 females with developing and immature oocytes according to the density of the setal bands surrounding the gonopores.

These Stage 2 females were carrying offspring and the maturity of the gonads indicated that they would probably spawn again in the following season; further evidence of spawning in successive years was obtained from mark-recapture records. Of six Stage 2 females with capture records in the brooding periods of 1977 and 1978, five carried eggs in both years; the other individual carried eggs in 1977, but only a spermatophore in 1978.

Body weights of Stage 0 and Stage 1 females examined in the laboratory (Fig. 3) overlapped in the 110–180 g range (60–72 mm CL) while Stage 1 and Stage 2 females overlapped in the 200–300 g range (75–85 mm CL). Similar trends were evident when frequencies of Stage 0, 1 and 2 were combined for all catches during the study period (Table 2), confirming the overlap in sizes of Stage 1 and 2 females suggested by the laboratory results. Substantial numbers of females in both stages occurred in the range of 70–95 mm CL, with the relative abundance of Stage 1 decreasing with increasing size.

In contrast to the results for gonosomatic index, ovarian maturity and setal stage, there was no apparent change in the relationship between gonopore diameter and carapace length. Gonopore diameters increased linearly in the range 50–90 mm CL ($Y = -0.027 + 0.044 X$, $n = 28$), but considerable variability was evident.

TABLE 2

Relative abundances of female *E. spinifer* in three maturation states (Stages 0,1,2) over the carapace length range recorded in all catches.

Carapace Length Class (mm)	Maturation Length 0	1	2
9.95–14.95	100*		
14.95–19.95	100		
19.95–24.95	100		
24.95–29.95	100		
29.95–34.95	100		
34.95–39.95	100		
39.95–44.95	100		
44.95–49.95	100		
49.95–54.95	100		
54.95–59.95	100		
59.95–64.95	100		
59.95–64.95	85	15	
64.95–69.95	14	82	4
69.95–74.95	4	70	26
74.95–79.95		35	65
79.95–84.95		25	75
84.95–89.95		34	66
89.95–94.95		17	83
94.95–99.95			100
99.95–104.95			100

* Abundance values are proportions of females (%) in each stage.

Males

Testis Structure

Each testis consists of two elongate, whitish lobes, slightly flattened dorso-ventrally, and joined towards the anterior end, adjacent to the points of exit of the vasa deferentia, by a broad commissure. In some individuals a second commissure is present mid-way along the testis length. Each vas deferens consists of two portions. The proximal portion is of constant, relatively small diameter, long, tightly coiled and convoluted to form a compact tubule mass lateral to the central portion of the gonad. The distal vas deferens is initially slightly convoluted, becoming relatively straight and increasing rapidly in diameter (Fig. 4).

In males with uninflated genital papillae (described below), the testes and vasa deferentia are small and inconspicuous, but in males with inflated papillae testes and vasa deferentia are much larger relative to the size of the individual; distal portions of vasa deferentia are noticeably distended over most of their length. In males with highly inflated papillae the testes are of similar relative size (compared with individuals with inflated papillae) and distal portions of vasa deferentia are relatively enormous, occupying much of the posterior half of the cephalothorax. In males with either inflated or highly inflated papillae the distal vasa deferentia contain large quantities of dense, white, glue-like spermatophore material, and account for much of the total gonad weight.

Papilla Structure

The gonopores of male *E. spinifer* are enclosed in membranous papillae on the ventral surfaces of the coxae of the fifth pereopods. Each papilla consists of a smooth membranous area, continuous with the arthrodial membrane of the coxa-basis articulation, and supporting an incompletely sclerotised ring, or crescent; details of structure and the three inflation stages are illustrated in Figures 5 and 6.

Uninflated genital papillae are flush with or only slightly raised above the general contours of the coxa, with the sclerotised ring closely adjacent over most of its length to the body of the coxa. In contrast, inflated genital papillae are distinctly raised above the general contours of the coxae, all membranous areas are distinctly tumid and the sclerotised ring separated from the body of the coxa by an obvious area of membrane. Uninflated and inflated genital papillae are otherwise similar, and some of the inflated papillae that are less tumid resemble uninflated papillae. Highly inflated genital papillae are conspicuous and unmistakable. These papillae are produced into turgid, balloon-like vesicles, often extending laterally past the coxa-basis articulation, with the sclerotised ring relatively small in size, displaced to the anteroventral surface of the papilla, and well-separated from the body of the coxa.

Gonosomatic Index

These results were plotted using a $\log_{10}$ scale for the index to provide an illustration in the same format as used for females. However, there were no clearly progressive relationships between gonosomatic index and body weight, so regression equations were not calculated. There were several distinct grouping of conditions of the genital papillae, gonosomatic index, and testicular maturity (Fig. 7). Males with uninflated genital papillae and body weights less than 45 g had immature testes, and had gonosomatic indices of approximately 0.1; specimens with inflated genital papillae and body weights over 130 g had mature testes as well as a gonosomatic index (0.5–1.5) that was variable but, on average, constant with carapace length. Individuals weighing 45–130 g had mature testes and either inflated or uninflated genital papillae. Animals with uninflated genital papillae had gonosomatic indices similar to those of smaller, immature males; however, indices of similar-sized individuals with inflated genital papillae were substantially greater, varied widely and attained the levels characteristic of larger mature males. Occasional individuals with aberrant numbers of gonopores were recorded.

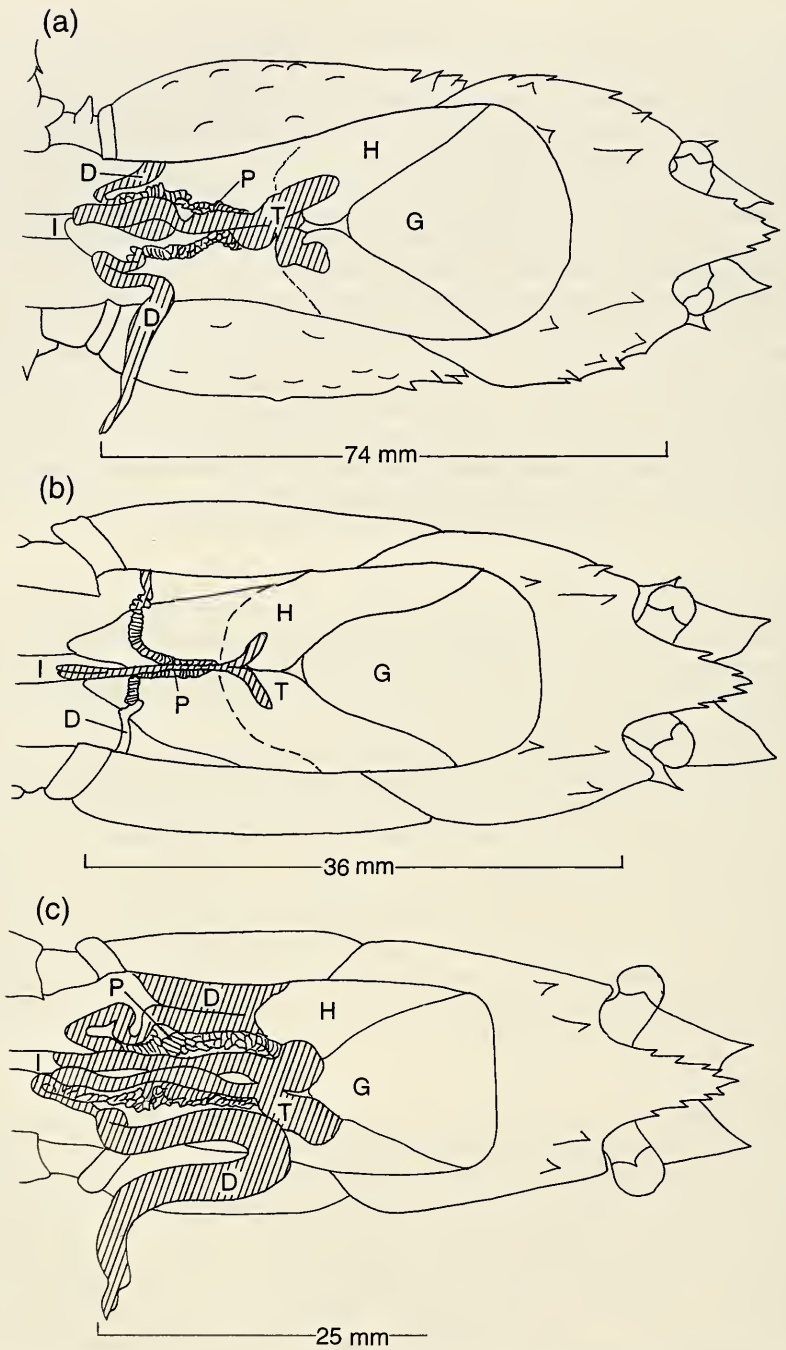

Figure 4. Anterior dorsal views of dissected *E. spinifer* males with different degrees of genital papilla inflation, showing testes and vasa deferentia *in situ*: (a) inflated papillae (normal mature); (b) uninflated papillae (normal immature); (c) highly inflated papillae (precociously mature). The dorsal walls of the carapace and abdominal segments, heart and dorsal blood sinuses, as well as the posterior dorsal gastric mill musculature have been removed. Key to symbols: D = distal vas deferens; G = gastric mill; H = hepatopancreas; I = hindgut; P = proximal vas deferens; T = testis.

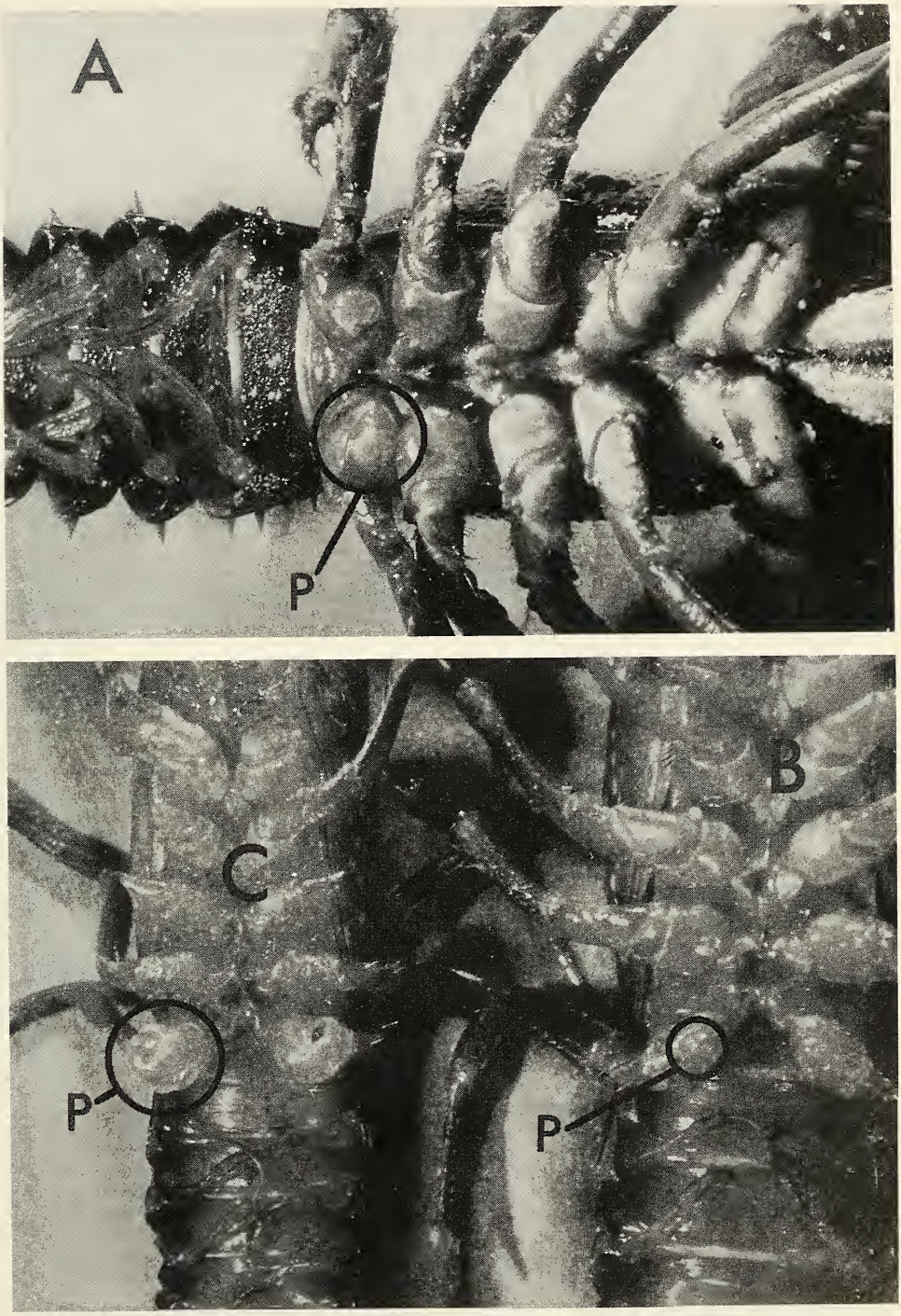

Figure 5. Ventral views of male *E. spinifer*, showing genital papillae: (A) inflated genital papillae (normal mature); (B) uninflated genital papillae (normal immature); (C) highly inflated genital papillae (precociously mature); P = genital papilla.

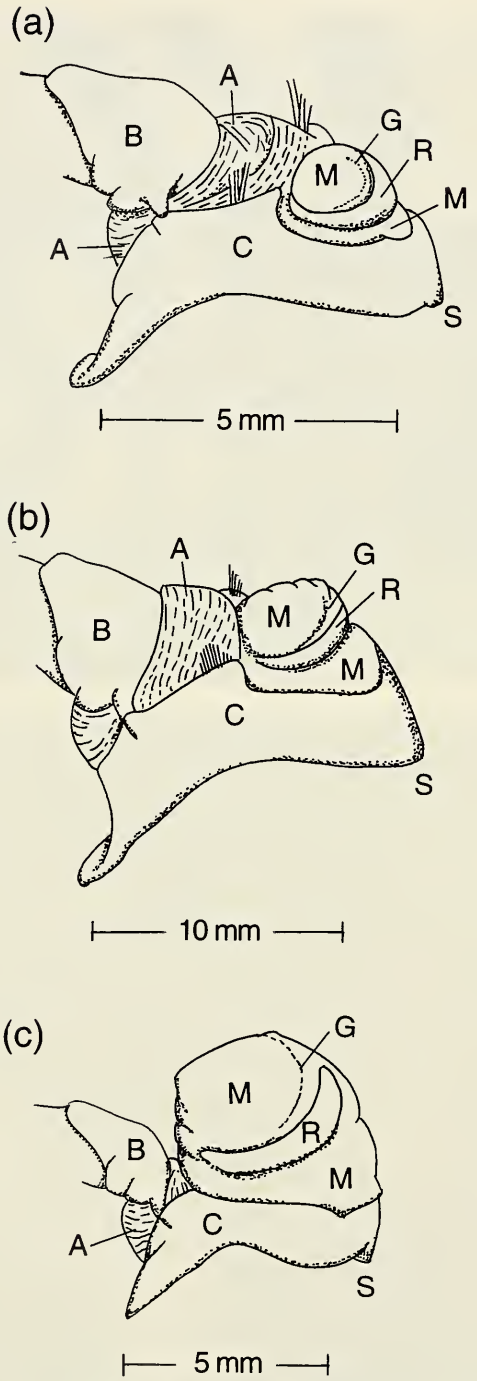

Figure 6. Degrees of inflation of the genital papillae of male *E. spinifer*. Coxa of the left fifth pereopod, anterior view: (a) uninflated (individual 36.6 mm CL); (b) inflated (individual 74.3 mm CL); (c) highly inflated (precocious individual 24.6 mm CL). Key to symbols: A = arthrodial membrane of the coxa - basis articulation; B = basis (or basipodite); C = coxa; G = gonopore; M = membranous part of papilla; R = sclerotised ring; S = articulation with sternum.

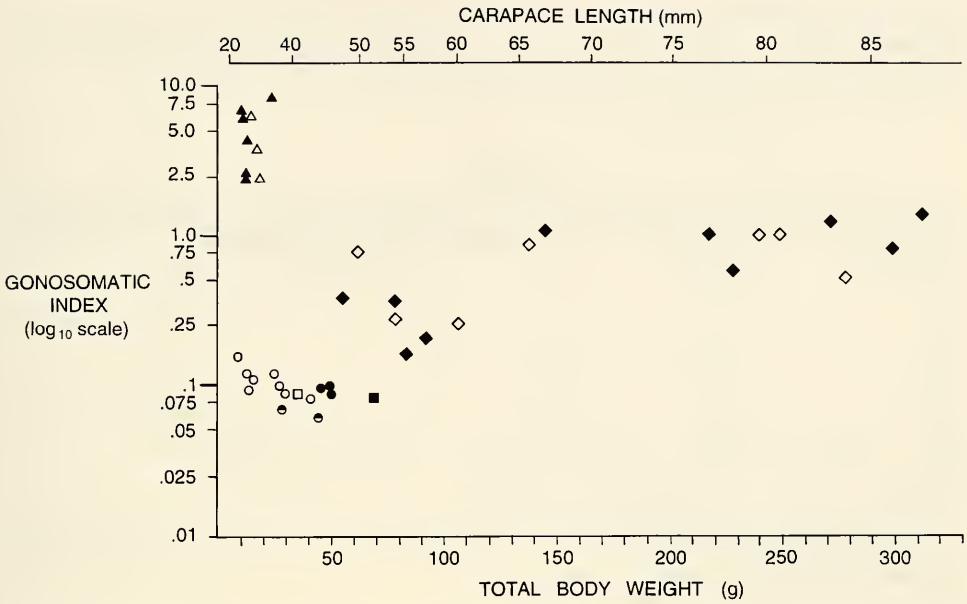

Figure 7. Relationships between gonosomatic index, testicular maturity, inflation of the genital papillae and body weight for male *E. spinifer*. Key to symbols: ● = papillae uninflated, testis immature; ○ = papillae uninflated, testis mature; ◓ = papillae uninflated, testis not examined; ◆ = papillae inflated, testis mature; ◇ = papillae inflated, testis not examined; ▲ = papillae highly inflated, testis mature; Δ = papillae highly inflated, testis not examined; ■ or ❑ = each individual with two male and two female gonopores.

Males with highly inflated genital papillae formed an entirely separate group. They were restricted to weights below 25 g, had mature testes and extremely high gonosomatic indices, two to ten times those calculated for mature individuals. Members of this group were designated as 'precocious' males.

Papilla Inflation and Size

Changes with carapace length in the relative abundances of males with uninflated, inflated or highly inflated genital papillae were similar in laboratory samples (Fig. 7) and all catches combined for the period of study; however, a major difference was that substantial numbers of larger males (CL >55 mm) with uninflated genital papillae were present in combined field data. Percentages of the two inflation categories varied considerably over this range, although variation was within sampling error except in the 60–65 mm size class; no sustained trends with CL were apparent.

Percentages with uninflated and highly inflated papillae were within sampling error at carapace lengths less than 25 mm, although calculations suggested a trend towards an increasing relative abundance of precocious males, over the range 10–25 mm (CL). Above 25 mm CL the relative abundance of males with highly inflated genital papillae decreased markedly and remained low up to the 40–45 mm size class; no males with highly inflated papillae were recorded above that size. The high relative abundance of individuals with uninflated genital papillae over 30–45 mm CL, rapidly decreased corresponding to the appearance of larger males with inflated papillae.

Recapture records (Table 3) indicated that genital papillae of males in the range 20–30 mm CL neither changed from the uninflated to the highly inflated condition nor reverted to the uninflated state. Although fewer data were available there was no evi-

dence of a different situation among larger individuals with highly inflated papillae. By contrast among very small males (<20 mm CL) there was some indication that genital papillae may have changed from uninflated to the highly inflated condition.

TABLE 3

Variation in the degree of inflation of the genital papillae of individual male *E. spinifer* with multiple recapture records.

Carapace Length (mm)	Mean Captures per male	Number of Individuals and Rating*			
		O	HI	I	O/I/HI
<20	2.8	2	6	–	1(O/HI)
20–30	2.5	69	29	–	–
30–40	3.4	63	3	–	–
40–60	4.1	21	1	4	8(O/I)
60+	3.1	2	–	12	6(O/I)

* Rating

O — genital papillae not inflated at all captures.

I — genital papillae inflated at all captures.

HI — genital papillae highly inflated at all captures.

O/I/HI — mixture of records as indicated.

Spermatophores, Fecundity and Early Development

Spermatophores appear as translucent, grey-white, irregularly-shaped masses of tough, gelatinous material; these are distributed patchily over the coxae of the fourth and fifth pereopods and adjacent sternal plates of large females. In section, each spermatophore consists of an amorphous matrix containing an irregularly distributed, highly convoluted tubule (0.05 mm diameter) containing the spermatozoa. Spermatophore material obtained from the distal vasa deferentia is white in colour, of thick but plastic consistency and extremely adhesive, setting rapidly after release.

Eggs are ellipsoid in shape; maximum and minimum diameters of individual eggs (n=50) ranged from 3.2–3.9 mm and 2.4–2.9 mm, with mean values of 3.5 and 2.7 mm. Eggs are attached (individually or in bunches) to the medial margins of the basipodites, all margins of the endopodites except the tips and to the proximal lateral margins of exopodites of all pleopods; attachment is by cords formed by several oosetae twisted together. This egg distribution corresponds to the occurrence of long oosetae, with the majority of eggs carried on the endopodite. Although both plumose setae and oosetae are present on the pleopods of mature females, eggs have not been observed attached to plumose setae.

The relationship between the number of eggs and carapace length for female *E. spinifer* (n=10) was well described by a straight line (Fig. 8). The regression slope was significantly different from zero ($t = 9.2$, d.f. = 8, $p < 0.001$), with carapace length accounting for 91% of the variance in egg number. Numbers of eggs for females from the study area ranged from 268 for an individual of 73.1 mm CL to 779 for a large adult of 103.6 mm CL. Additional data were obtained for five females collected from the Hacking River near Otford, in an adjacent catchment; egg numbers ranged from 534 for a female of 82.9 mm CL to 1299 for a female of 109.4 mm CL.

The maroon yolk of oocytes becomes darker during the later development of fertilised eggs. During early development the blastopore is visible to the naked eye as a small dark spot; later the embryo becomes visible as a white patch at the pole of the egg,

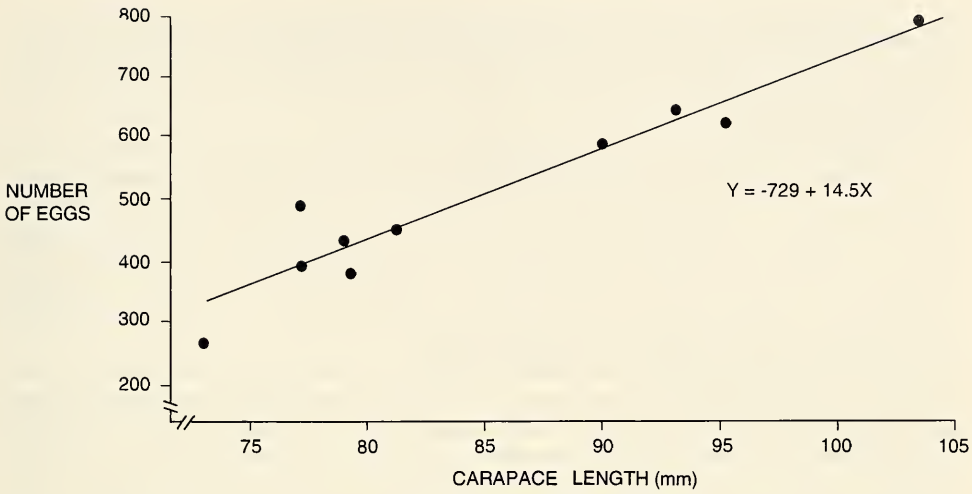

Figure 8. Relationship between the number of eggs and the carapace lengths of female *E. spinifer* (n = 10: 70–105 mm CL).

opposite its point of attachment to the parental pleopod. Early larval development is completed within the egg and young hatch as Stage 1 juveniles; post-embryonic development continues with Stage 1 moulting to become Stage 2 juveniles. With a further moult these become Stage 3 juveniles, identical in form to adults except for the progressive development of body spines and an increase in robustness with size.

Overall morphology of Stage 1 and 2 juveniles is as described for other parastacids (Hamr 1992); and observations of captive stocks (at ~20°C) indicate that Stage 1 juveniles are attached to the egg membrane by a thread running from the telson for a period of at least several hours after hatching. One day after hatching these threads are no longer apparent. Both Stage 1 and Stage 2 juveniles are attached to the setae of parental pleopods by recurved hooks; one hook extends proximally, in the medial plane, from the distal dactylus of the fourth and fifth pereopods. These hooks close onto a series of serrations on the body of the dactylus, firmly gripping the setae.

Brooding females held in captivity began to devour their offspring after periods ranging from several days to several weeks, and offspring had difficulty in hatching and moulting when detached from their mother. It was not possible to accurately estimate duration of stages in a particular brood; however, observations of offspring at different stages, on different females, suggested that development on a given female was synchronised to within a period of several days. Detailed observations on two captive females indicated that all Stage 3 juveniles departed voluntarily from the parent over a period of three to four days, although prior to this many juveniles made short excursions over and away from the parent.

Annual Reproductive Cycle

Periods of the year during which mating, spawning, incubation, hatching and departure of juveniles occurred were inferred from the relative abundances of females in different brooding states. Numbers of females captured at monthly samplings were often small and not all 31 months for the study period (1976–78) were represented; however, available data indicate that trends, in numbers of females at particular brooding states, were similar for each of the three years.

The majority of mature females mated during May, and were observed carrying spermatophores in early June. Spawning typically occurred during June, and the majority of females carried eggs in early July. The percentage of females that retained spermatophores after spawning was initially high at around 60% in early July, declining to zero by early October.

Eggs of most females hatched during October and a majority of mature females carried Stage 1 juveniles in early November. Stage 1 juveniles moulted during early November, and all captured females carried Stage 2 juveniles during mid-November. Stage 2 juveniles moulted during late November, and the majority of females carried Stage 3 juveniles in early December. Of the two non-brooding females captured in early December one had traces of egg attachments on the pleopods. One of the brooding females had already released the majority of her offspring but none of the females captured in mid-late December were carrying juveniles.

These data indicate that reproduction in the *E. spinifer* population at the study area followed a fixed, annual cycle, and events in the annual reproductive cycle of the majority of females were synchronised to within a period of a few weeks. Water temperature also followed an annual cycle (Fig. 9) and events in the annual reproductive cycle coincided with changes in water temperature that were similar for each year. Mating occurred as water temperatures fell rapidly below 14–15°C, spawning occurred as water temperatures approached the annual minimum of 10–11°C, while juveniles were released as water temperatures attained the annual maximum (20–24°C).

DISCUSSION

Study Area

The Loddon River was selected for accessibility, the permanence of the stream and the large crayfish population. Although it may be typical *E. spinifer* habitat, in terms of stream bed topography and substrate types or aquatic vegetation, the site may also be considered atypical in two respects.

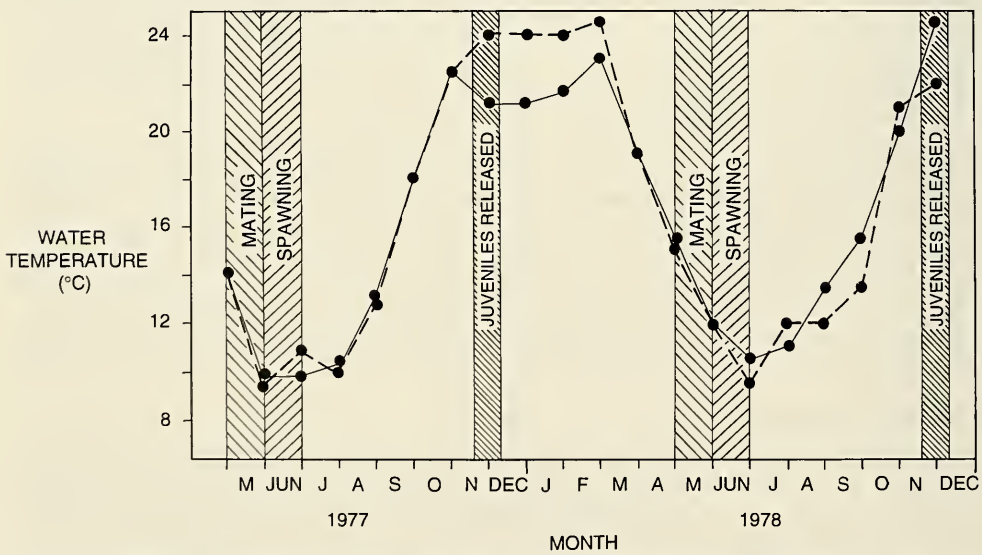

Figure 9. Summary of annual water temperatures related to key events in the annual reproductive cycle of *E. spinifer* from Pool 3 (– –) and Pool 7 (—) on the Loddon River.

Firstly, the terrain is relatively flat and study pools are near the river source. So the flooding that did occur probably had less impact than on typical sandstone streams of the region, which are characteristically steep and flowing through rocky gullies. Secondly, the adjacent swamps and high local rainfall probably provide a more continuous input of water than most streams around Sydney receive; the pools did not have the dramatic reduction in water level associated with many sandstone streams during dry periods. So the hydrologic environment in the study area is abnormally constant over the year.

Maturation

Females

The ovaries of *E. spinifer* are of typical decapod form (Barnes 1987), although the tubular, anterior extensions (additional lobes) lateral to the cardiac stomach, described in *Cherax tenuimanus* (Morrissy 1970) and *C. destructor* (Johnson 1979), have not been observed. Colour and the degree of yolkiness provide a rapid means of assessing the state of development of ovaries and identifying immature as well as incipiently mature or mature females, without histological examination.

Allocation of females to three Stages, on the basis of setal development around the gonopores, during May-June resulted in complete segregation of mature and immature individuals. The immature ovaries and single, linear progression in gonosomatic indices for Stage 0 and 1 females indicated that the initial appearance of setae, around the gonopores, was not related to any immediate change in reproductive condition.

The Stage 2 female captured during May–June with a developing ovary was not considered an example of inconsistent allocation. The ovary of this individual differed from all Stage 1 females captured at the time and was similar to Stage 2 ovaries. Incomplete yolk deposition in this female may have been associated with delayed spawning, or with failure to spawn.

Combined laboratory and field examinations showed a very low incidence of incorrect allocation on setal development; each individual for which inconsistent stages were recorded had also been allocated to the normal stage on other occasions. None of the inconsistencies were related to changes in setal development at moulting; in addition, some gradation in the degree of setal development between stages was noted. Inconsistent allocations of Stage 2 to Stage 1 or Stage 1 to Stage 2 occurred with similar frequencies. So an incorrect allocation could be expected once for every 40 examinations; the single inconsistent allocation of a Stage 0 female to Stage 1 was probably a recording error.

The discussion of Stage 1 females has been based on collections during May-June; however, ovaries of females collected during November-December indicated that a substantial proportion in Stage 1 were incipiently mature and likely to spawn in the next season. Females larger than 55 mm CL (including all those in Stages 1 and 2) were found to moult once per year, during March-April (Turvey and Merrick 1997b). As no Stage 1 females were observed to be carrying eggs, it is concluded that incipiently mature females moulted during March-April and assumed Stage 2 characteristics prior to their first spawning.

The inability to distinguish between immature and incipiently mature females in Stage 1, on the basis of gonopore setae, has several implications. If individuals are examined between the annual moult and the commencement of spawning, then all females likely to spawn in that year will be Stage 2. Similarly, for females captured at other times, all that spawned during the previous season will be in Stage 2. But, given the high proportion of Stage 1 females that were incipiently mature, numbers of Stage 2 females taken outside the period between annual moult and spawning would probably be a gross underestimate of those likely to spawn during the next season.

The overlap in CL ranges of females in Stages 1 and 2 (Table 2) indicates considerable variation in the size at which individuals attain maturity. Only one mature specimen was recorded in the 65–70 mm CL group; however, substantial numbers of mature females were present in the 70–75 mm class. The percentage of mature individuals increased rapidly above this size, but 100% maturity was not attained until females exceeded 95 mm CL.

Variability in the size of females at maturity has also been noted for other parastacids (Honan and Mitchell 1995a; Morrissy 1975); however, maturity in many decapods is not simply a function of size. Chittleborough (1974) concluded that the variable size of female lobsters *(Panulirus longipes cygnus)* resulted from variation in growth rates, with maturity being attained at a specific age. The same may apply to *E. spinifer*, as growth rates did vary, resulting in a wide range of estimated sizes at any given age (Turvey and Merrick 1997c). As it was not possible to determine ages of individual females, the relationship with maturity could not be clarified.

The data suggest that the majority of mature female *E. spinifer* spawned each year after reaching maturity; factors contributing to this conclusion were the percentage of individuals known to have spawned in both 1977 and 1978, as well as the ovarian condition of adults carrying juveniles in November-December. Honan and Mitchell (1995a) reported that over 95% of mature *E. bispinosus* females bred each season.

It was the observations of Ryder (1972), on *E. australasiensis,* that initially stimulated investigation of a possible link between gonopore setae and maturity. During this study gonopore setae, similar to those of *E. spinifer,* were also observed in large female *E. armatus, E. hirsutus, E. hystricosus* and *E. valentulus.* In each instance the full development of gonopore setae (Stage 2) was associated with females carrying eggs. Detailed analyses were not undertaken, but it is suggested that the setal development stages devised for *E. spinifer* might indicate maturity in other species; although, Honan and Mitchell (1995a) did not find setation a reliable maturity indicator in *E. bispinosus.*

The structure of *E. spinifer* oosetae and their distribution on pleopods is similar to that described for other parastacids (Johnson 1979; Morrissy 1975); egg distributions were also similar to those reported previously, with the majority of eggs carried on the endopodites. Despite their small size (requiring microscopic assessment), oosetae must be considered a primary sex characteristic; they performed the function of attaching eggs to pleopods and were present only on mature or incipiently mature females. But in the absence of any observed function, the gonopore setae are probably a secondary sex characteristic.

Gonosomatic indices of mature *E. spinifer* females, collected in May-June, ranged from 2.3–4.2. Johnson (1979) calculated similar indices (from 0.9–3.5) for *C. destructor* with ovaries in the later stages of maturation, but for individuals just prior to spawning, the values exceeded 3.5 (up to 5). So these two species apparently have similar allocations of body tissue to reproduction.

No further comment is possible on quantitative relationships between gonopore size and carapace length; Honan and Mitchell (1995a) used different qualitative features (level compared with coxal surface, calcification, rim incisions) to rate gonopores in relation to maturity in *E. bispinosus.*

Males

The gonads of all males are similar in form, apart from differences in proportions; they are also similar in overall morphology to that reported for other astacuran decapods (Farmer 1974; Johnson 1979).

In normal males there is a progressive acquisition of mature characteristics with increasing size. Initially individuals have a low gonosomatic index, immature testis and uninflated genital papillae. The first sign of incipient maturity is maturation of the testes,

without any substantial increase in gonosomatic index or papilla inflation. This is followed by a simultaneous inflation of genital papillae and rise in gonosomatic index, to a level which is maintained with further increase in carapace length.

In individuals with high gonosomatic indices and inflated genital papillae, the distal vasa deferentia are turgid with large quantities of spermatophore material,and contribute a substantial proportion of the total gonad weight; the increased gonosomatic index is considered to be due to spermatophore production. Only males that produced spermatophore material could be considered reproductively functional. Normal males with mature testes but uninflated genital papillae were designated as immature and inflated papillae were considered to be indicative of functional maturity.

The carapace lengths of functionally mature and immature normal males overlapped in the 55–70 g range (45–55 mm CL) and it is concluded that normal males become functionally mature over this range. Gonosomatic indices typical of large males were generally attained at body weights exceeding 140 g (~65 mm CL), indicating that maximum spermatophore production may not have occurred until individuals were considerably larger than the size at which they first matured.

Individuals with three or four gonopores are not uncommon among Australian parastacids (Horwitz 1990; Johnson 1979) and are often functional males. *E. spinifer* with aberrant gonopores, from the Loddon River, displayed charactersitics typical of males; furthermore, Honan and Mitchell (1995a) found that frequencies of aberrant gonopore configurations varied widely between *E. bispinosus* populations.

Analyses of Loddon River males, collected during the mating season indicate the presence of a second group of 'precocious' functional males (Fig. 7). Gonosomatic indices of precocious males were considerably greater than those of normal males; their vasa deferentia were extremely large (relative to size of animal) and filled with spermatophore material. Precocious males were functionally mature at a size considerably below that of the smallest normal male. Apart from the highly inflated genital papillae, precocious males retained the appearance of small *E. spinifer* of both sexes, showing no external differences either in body proportions or development of spines.

Multiple recapture records (Table 3) indicated that the highly inflated condition of genital papillae was fixed once it had been attained; nor did immature normal males assume the precocious condition at carapace lengths greater than 20 mm, so above this size male *E. spinifer* were dimorphic. They were in either the fixed, precociously mature condition, or were immature, attaining maturity at 45 mm CL or above.

Increases in relative abundance of males (10–20 mm CL) with highly inflated genital papillae suggested that immature normal males may have assumed the precocious condition over this size range. Only a small number of individuals of this size were captured more than once during the study, but the papillae of one are known to have changed from the uninflated to the highly inflated condition. It should also be emphasised that the smallest precocious male captured had a carapace length of 12.0 mm and was among the smallest individuals recorded. It is possible that some males may be precociously mature at smaller sizes.

Dimorphism in the size of males has been recorded for other decapods. In dense populations of the freshwater prawn (*Macrobrachium rosenbergii*), differential growth patterns have been detected and the presence of very small sexually mature individuals has been demonstrated (Barki et al. 1991a,b; Karplus et al. 1991). The only report of male dimorphism in a parastacid is a general comment by Morgan (1997), about small males (with the features of the precocious group) being present in a number of *E. spinifer* populations.

Observations of captive specimens indicated that precocious males were capable of mating with mature females, in the absence of other males (Turvey 1980); however, the contribution of precocious males to successful mating in the Loddon River population is not known. The possible significance of these two male forms for *E. spinifer* is discussed

in population studies (Turvey and Merrick 1997a), which consider sex ratios and overall size structure, relative abundances of both types of functional male as well as recruitment and origins of the precocious group.

Spermatophores, Fecundity and Early Development

E. spinifer spermatophore structure is similar to that described for another local parastacid *(Cherax destructor)* by Johnson (1979). Mason (1970) considered that sperm were released when the spermatophore dissolved during spawning in the astacid *Pacifastacus trowbridgii*, but the mechanism of sperm release for fertilisation in *E. spinifer* is unknown.

As other freshwater crayfishes do, *E. spinifer* produces large yolky eggs which hatch at a late stage of development. *E. spinifer* eggs were similar in shape and size to those of other parastacids (Hopkins 1967; Johnson 1979; Morrissy 1970; Ryder 1972; Shipway 1951a): they were also attached to the pleopods in the same way. An approximately linear increase with carapace length in the number of eggs carried by females has also been described for other parastacid species (Hopkins 1967: Johnson 1979; Morrissy 1970); recorded fecundities are similar to ranges reported for other *Euastacus* (Table 1).

Yolk colour in the eggs of several other parastacids has been reported to change during development (Hopkins 1967; Johnson 1979; Ryder 1972); however, this does not occur in *E. spinifer*, except for a slight darkening.

The early embryonic development as well as larval attachment, morphology and number of juvenile stages after hatching are typical of Australasian parastacids (Hamr 1992; Hopkins 1967; Johnson 1979; Ryder 1972; Shipway 1951a; Suter 1977). The terminal teeth of the chelae and antennal scale spines of Stage 1 and 2 juveniles may have been similar to the 'hooks' described for other parastacids (Clark 1937; Hopkins 1967; Suter 1977), but were not used for attachment in *E. spinifer.*

Development of the offspring on individual females was synchronous to within a few days, up to and including the departure of juveniles from the mother. Females collected in early December had released most larvae indicating that the release of Stage 3 juveniles commenced during late November. Lack of any *E. spinifer* carrying in mid or late December indicated that release of juveniles was normally completed in early December; a similar observation of developmental synchrony has been made for *Cherax destructor* (Johnson 1979).

Annual Reproductive Cycle

The interval between mating and the appearance of eggs indicates that spermatophores may have been carried for a month or longer, before spawning occurs. It is also clear that spermatophores are not completely removed at spawning and may be retained for another month or more. *E. spinifer* differs considerably from *Cherax destructor* (Johnson 1979), in which spawning usually commences within a few hours of mating, and spermatophores are present for no more than a few days. Although the durability of *E. spinifer* spermatophores would be advantageous in preventing loss or damage due to abrasion against rock substrata, the long period between mating and spawning cannot be explained.

Females of a number of *Euastacus* species carrying eggs in early stages of development have been observed during the month of May (Table 1). These observations include *E. spinifer* in the Hacking River, a separate drainage basin north-east of the study area (Turvey 1980). The data available suggest that *Euastacus* typically spawn in late autumn throughout much of the eastern coastal range of the genus; but *E. spinifer* in the Georges River near Campbelltown, in the adjacent catchment north-west of the study area, spawned during early September in both 1975 and 1978 (Turvey 1980).

Female *E. spinifer* incubated eggs for approximately 110–140 days over winter prior to hatching; similar, or longer, incubation periods have been reported for a number of *Euastacus* species (Table 1). From the field records it is estimated, in *E. spinifer*, that the total period between hatching and the departure of juveniles from the mother is between four and ten weeks; Honan and Mitchell (1995a) also reported a larval period of about four weeks in *E. bispinosus*.

Control of reproductive cycles by temperature and/or photoperiod has been proposed for other freshwater crayfishes (Aiken 1969; Merrick and Lambert 1991), but Sastry (1983) suggested that a complex of factors was involved. Honan and Mitchell (1995a) also contend that the breeding pattern is unlikely to be determined by a single environmental variable. Whilst events in the *E. spinifer* cycle, in the study area, were certainly closely associated with water temperatures, they could also be correlated with photoperiod or other environmental parameters showing annual periodicity. Honan and Mitchell (1995a) reported that *E. bispinosus* also mated when water temperatures were 15°C and falling; hatching occurred as temperatures exceeded 15°C and *E. bispinosus* also released juveniles at about 20°C.

Annual reproductive cycles of parastacids generally fall into two groups, those with a relatively short incubation period during the warmer months (summer brooders), and those with a long incubation period over winter (Honan and Mitchell 1995a). Some summer brooders only breed once while others may reproduce for several years (these include the commercial *Cherax* species). Whereas winter brooders may breed annually or biennially for a number of years (Honan and Mitchell 1995a). This study indicates that *E. spinifer* is a winter brooder.

Life Cycle Strategy

Broadly, the reproductive biology of *Euastacus spinifer* conforms to the pattern emerging for the genus. Details of anatomy, egg structure and attachment, fecundities, developmental stages and the timing of the annual breeding cycle are similar to data available for other *Euastacus* species. Small differences include the delay between mating and spawning and the fact that eggs do not change colour as they develop. The most unusual reproductive feature of the Loddon River population was the presence of small, precocious males.

The different life cycle traits exhibited by females or normal males and precocious *E. spinifer* males could be interpreted as separate strategies designed to cope with different sets of environmental conditions. The K-strategy (to maximise the ability to compete and avoid predation) seems to apply to females and normal males. Features associated with this selection include delayed reproduction, large maturity sizes, brood care and individual longevity (Stearns 1976). By contrast, the r-strategy or selection favours increased reproductive output in fluctuating environments; associated features include early reproduction and small size at maturity (Stearns 1976).

So r- selection apparently fits the available results for precocious males. But it is unclear how two sets of traits, selected for by different sets of environmental conditions, could develop and be maintained in one population especially when the previously documented stability of the Loddon River habitat is considered. Perhaps social interaction within the population contributes to the male dimorphism, as it is known to do in *Macrobrachium rosenbergii* (Karplus et al. 1991).

The level of incidence of precocious males in *Euastacus spinifer* populations is unknown and general conclusions about the species have to be based on normal males and females. In summary, the Sydney crayfish *(E. spinifer)* is slow to mature at a relatively large size, breeds annually in a synchronised cycle for each population, has low fecundity and limited recruitment. The success of this life cycle strategy depends on long-lived individuals, breeding repeatedly over a number of years and low natural mortality.

ACKNOWLEDGMENTS

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